PROC. ENTOMOL. SOC. WASH.
91(1), 1989, pp. 26–28

THE INS AND OUTS OF A TROPICAL SOCIAL WASP NEST

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Abstract.—An extraordinarily large nest of the social wasp *Synoeca septentrionalis* is recorded from Costa Rica. The wasps had formed two holes through which they could enter or leave the nest, unlike the usual single-hole condition in the genus. A statistical test shows that one nest-hole was preferentially used for entering and the other for leaving, which presumably increased the colony's traffic efficiency. It is postulated that this tendency was a statistical result of small individual behavior differences, so that it need not require any organizing mechanism at the colony level.

Key Words: nest, *Synoeca*, Vespidae, wasp

Vespine and swarm-founding polistine wasps (Hymenoptera: Vespidae), except for the small genus *Apoica*, characteristically nest either in secure cavities or, more commonly, construct an envelope around the brood-combs (Jeanne 1975, Wenzel, in press). This allows them to restrict access to the interior of the nest. There have been occasional observations of nests with two or more entrance holes (Chopra 1925, Maidl 1934, Richards and Richards 1951, R. S. Jacobson, pers. comm.; pers. obs.), and Réaumur (1722) intimated that it is usual for *Vespula* sp. (probably *V. germanica* and/or *vulgaris*) nests to have two holes. It now seems certain, though, that all social wasps and bees with regular envelopes characteristically have one entrance hole. This is apparently taken for granted, although the nests of ants and termites often have many such holes.

Synoeca septentrionalis Richards is a widespread, conspicuous, swarm-founding polistine of Central and South America (Richards 1978). Its nest begins as a single comb flat against a tree trunk or limb or other substantial surface, surrounded by a domed envelope with prominent ridges running across it and typically with a round hole at the high end. As the colony grows, it may add a new lobe to the nest at the high end, obscuring the old hole and replacing it with a new one on the new lobe. I have seen occasional nests with two or three lobes in Costa Rica; Rau (1933) mentioned a five-lobed nest in Panama, and Buysson (1906) figured one from Mexico with six lobes, apparently the largest nest reported for the genus.

In early 1979, on a large fig tree (*Ficus* sp.) near the headquarters of the Santa Rosa National Park of Costa Rica, I found an active *S. septentrionalis* nest with two remarkable features. First, it consisted of nine lobes with a total length of about 3 meters (Fig. 1). Second, it had paired holes, each of the usual form and in the usual position (Fig. 2), with a combined perimeter of about 10 to 12 cm.

Réaumur (1722) reported that *Vespula* workers consistently enter through one of the two nest-holes and leave through the

Fig. 1. Nine-lobed nest of *Synoeca septentrionalis* in Santa Rosa National Park, Costa Rica. It is on the underside of a large branch at an angle of about 60° from horizontal.

Fig. 2. The uppermost lobes of the nest, showing the two entrance holes. Wasps on the envelope are about 20 mm long.

other. Although the quantitative study of behavior was nearly unknown in his time, we know that Réaumur made original observations on *Vespula* colonies, and it is reasonable to suppose that he found at least one nest with two holes and watched it long enough to gain an impression of directed traffic. Indeed, if a colony has considerable traffic through a bottleneck, it makes biological sense that any separation of the inward and outward streams will increase the efficiency of passage. Accordingly, I predicted that the very large Santa Rosa *Synoeca* colony would preferentially treat one of its two nest-holes as an entrance and the other as an exit.

Traffic at the nest was usually so heavy that I could not simultaneously monitor the direction of movement through both holes. In each of eight observations periods, I sequentially recorded a) the hole-choice of 50 wasps without regard to whether they entered or left the nest, b) direction of passage of 25 wasps at one hole, and c) direction of 25 wasps at the other hole. The observation periods were at various times when the wasps were active over the course of 10 days and totaled about two hours.

The hole-choice results (a) show greater use of the right-hand hole, which was the site of 280 (70%) of the 400 movements. The direction-of-passage data (b and c) show apparently more wasps leaving than entering the nest (Table 1). If the hole-choice bias is entered as a correction factor (e.g. by multiplying the left-hole figures by $\frac{3}{7}$ *or* the right-hole figures by $\frac{7}{3}$ in Table 1), though, the overall inward and outward traffic during the observation time is found to be almost

Table 1. Cumulative numbers of wasps leaving and entering the nest out of 25 moving through each hole during each of eight observations periods.

	Left Hole	Right Hole	Total
Entering	64	114	178
Leaving	136	86	222
Total	200	200	

Table 2. Percentage breakdown of total traffic during the observation time. Based on Table 1 and the hole-choice results, as explained in text.

	Left Hole	Right Hole	Total
Entering	9.6	39.9	49.5
Leaving	20.4	30.1	50.5
Total	30.0	70.0	100.0

identical. Table 2 thus gives the percentage breakdown of the traffic which would presumably have been recorded if I had been able to monitor all passages at once.

The bias-corrected results show a significant difference between the two holes in the directional distribution of traffic (Chi-square, $P < 0.01$). As seen in Table 2, it is equivalent to what would be recorded if 20% of the wasps consistently leave the nest by the left hole and return by the right hole, while the other 80% each tend to leave and return by the same hole.

There is some indication in *Synoeca* spp. of an unusual flexibility in nest construction (Vecht 1967, Overal 1982), which may account for this nest's two-holed condition. It makes little difference here whether this originated and was maintained as an adaptive response to extraordinarily large colony-size or through ordinary building errors. On the other hand, the origin of the tendency toward a plausibly more efficient flow of traffic is pertinent. There is no evidence for a higher organizing mechanism in *Synoeca* which could account for this, and we need not postulate any. The most parsimonious hypothesis is that the small behavioral differences which unavoidably arise between individuals have been summed to produce a meaningful phenomenon at the colony level.

Acknowledgments

My stay in Costa Rica was supported by a graduate assistantship from the Department of Entomology, University of Georgia. A grant-in-aid from Sigma Xi provided research supplies. I am grateful to Jorge Morales and other staff of the National Parks Service of Costa Rica for making it convenient and pleasant to work in Santa Rosa. Criticism from Bob Jeanne, John Wenzel and the journal's reviewers led to substantial improvements in the paper.

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